

B R E V I O R A

Museum of Comparative Zoology
MUSEUM ZOOLOGICAL LIBRARY

US ISSN 0006-9698

JAN 7 1974
CAMBRIDGE, MASS. 28 DECEMBER 1973

NUMBER 412

HARVARD UNIVERSITY
MYLOSTOMA VARIABLE NEWBERRY,
AN UPPER DEVONIAN DUROPHAGOUS
BRACHYTHORACID ARTHRODIRE,
WITH NOTES ON RELATED TAXA

WILLIAM J. HLAVIN¹
and
JOHN R. BORESKE, JR.²

ABSTRACT. All known gnathal elements of the durophagous arthrodire *Mylostoma* from the Late Devonian (Famennian) Cleveland Shale of Ohio show that the inferognathal and posterior palatopterygoid elements increase in size and maintain a constant shape during growth, while the anterior palatopterygoids are paired elements in the juvenile condition which fuse into a single median gnathal in the adult. *Dinognathus* is a synonym of *Mylostoma*. *Mylostoma variable*, *Mylostoma eurhinus*, and *Mylostoma newberryi* are here considered the only valid taxa. *Mylostoma eastmani* from the Grassy Creek Shale of Missouri (Famennian) is now considered a synonym of *M. variable*; it was based on undiagnostic gnathal characters. The fusion of anterior gnathal elements is suggested as a possible origin of the median gnathal in the enigmatic arthrodire *Bungartius* and possibly also in the selenosteid *Paramylostoma*.

INTRODUCTION

Newberry (1883: 146) described a left inferognathal from the Cleveland Shale member of the Ohio Shale Formation (Late Devonian, Famennian) as *Mylostoma variable*, referring to it as a "dipterine ganoid" on the basis of the similarity of its gnathal element to those of *Dipterus* and *Ceratodus*. In 1893, a concretion containing the virtually complete cranial, thoracic, and

¹Cleveland Museum of Natural History, Cleveland, Ohio, and Boston University, Boston, Massachusetts.

²Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts.

ventral shield of a single individual was collected from the Cleveland Shale exposures at Brooklyn, Ohio, and was obtained by the American Museum of Natural History, with the counterpart being acquired by the Museum of Comparative Zoology. Dean (1901) described both specimens as *Mylostoma variable*, placing the taxon within the Arthrodira. Eastman (1906) reviewed the jaw mechanics of *Mylostoma* as well as the morphology of its gnathal elements and concluded that *Mylostoma* was an arthrodire with a gnathal apparatus specialized for crushing.

Hussakof (1909: 268) described *Dinognathus ferox* as "an imperfectly definable genus and species of arthrodire" on the basis of an isolated median gnathal. Eastman (1909) made a hypothetical reconstruction by placing the *Dinognathus ferox* type of dentition over the inferognathals of *Mylostoma terrelli* and placing the posterior palatopterygoids of *M. terrelli* on the labial side of the *Dinognathus ferox* median gnathal. Dunkle and Bungart (1945) described *Dinognathus eurhinus*, a second species of *Dinognathus*, on the basis of a median gnathal with general morphology differing from that of *D. ferox*, but with features giving evidence for a similar function.

A recently discovered specimen (CMNH 8120) represents a complete set of jaw elements of an adult *Mylostoma variable*. This specimen, along with other specimens in the Museum of Comparative Zoology (MCZ), American Museum of Natural History (AMNH), Oberlin College (OC), and the Cleveland Museum of Natural History (CMNH) has enabled this study of the morphology of the functional region of the inferognathals and palatopterygoids through various size-growth stages. Evidence of the fusion of the anterior palatopterygoids has been observed in the adult, aiding in the synonymy of mylostomatid taxa that were based on undiagnostic character-states of the anterior palatopterygoids.

ORDER ARTHRODIRA

FAMILY MYLOSTOMATIDAE

Mylostoma variable Newberry, 1883

Mylostoma variable Newberry, 1883: 146

Mylostoma terrelli Newberry, 1883: 147

Dinognathus ferox Hussakof, 1909: 268

Mylostoma eastmani Branson, 1914: 62

Holotype. OC 1300, left inferognathal.

Paratypes. MCZ 1435, left anterior palatopterygoid; MCZ

1436, right posterior palatopterygoid; AMNH 42G, left anterior palatopterygoid; and AMNH 43G, right anterior palatopterygoid.

Type locality and horizon. Sheffield Lake, Ohio. South Shore of Lake Erie, T 7 N, R 17 W, Lorain County, Ohio; Cleveland Shale member of the Ohio Shale Formation.

Age. Famennian (Late Devonian).

Hypodigm. Cleveland Shale member of the Ohio Shale Formation, Ohio: AMNH 7526, nearly complete disarticulated cranial and thoracic shields (counterpart = MCZ 1490); CMNH 8129, left and right inferognathals, left and right posterior palatopterygoids, median gnathal; AMNH 7915, 10701, CMNH 6094, median gnathals; MCZ 1429–1431, CMNH 5080, 5150, 5177, 6095, 6224, 7256, 7643, 7705, OC 1483, inferognathals; AMNH 44G, 3290, 3588, 3591, MCZ 1437–1438, 13271–13274, OC 1301, 1429, CMNH 5022, 5795, 7694, palatopterygoids. Huron Shale member of the Ohio Shale Formation, Ohio: MCZ 13275, right inferognathal. Grassy Creek Shale Formation, Missouri: University of Missouri collections, median gnathal, posterior palatopterygoid.

Revised diagnosis. Cranial shield having a wide lateral width and short anteroposterior length similar to that of the titanichthyids. Postorbital element bordered posteriorly by paranuchal; centrals not in contact with marginals and are anteriorly separated by pineal. Anterior palatopterygoids of juvenile fuse to form median gnathal in adult. Suborbitals narrow and long, orbits large. Median dorsal short without well-developed keel. Median gnathal of *Mylostoma variable* possessing a greater width than length and less deeply excavated on either side of the longitudinal ridge than that of *Mylostoma eurhinus*.

SYSTEMATIC DISCUSSION

The holotype of *Mylostoma variable* Newberry (1883: 146) is a left inferognathal, the size of which indicates that it belongs to a young adult of the species. The paratypes, comprising the anterior and posterior palatopterygoids, are characteristic of the known palatopterygoids of *Mylostoma*. Dean (1901) described the most completely known specimen of *M. variable* (MCZ 1490, AMNH 7526). This specimen represents a young individual of the species (Plate 1). All of the elements comprising the upper and lower jaw apparatus are well preserved and are

the basis for Eastman's (1907) reconstruction of the mylostomatid dentition.

A second species, *M. terrelli* Newberry (1883: 147), represents the left inferognathal (MCZ 1430) of an individual larger than the holotype of *M. variabile*. Hussakof (1909: 268) believed the specific variations in this specimen could be attributed only to an age difference in *M. variabile*, and recommended that *M. terrelli* become a synonym of *M. variabile*.

A third species of *Mylostoma*, *M. newberryi* Eastman (1907: 224) is based on a pair of dental elements identified as the anterior portions of left and right inferognathals (OC 1302) and the posterior portion of a smaller left inferognathal (MCZ 1439). These dental elements were originally described by Newberry (1889: 165) as belonging to *M. variabile* because of their distinctive narrowness and triangularity, which he believed demonstrated diversity in the species. Earlier, Eastman (1906: 22; fig. E) figured these plates as pre-anterior palatopterygoids as part of his reconstruction of the upper dentition of *M. variabile*. This reconstruction is misleading since these pre-anterior palatopterygoids are not present in the MCZ 1490 and AMNH 7526 specimens. We believe that Eastman realized this a year later and established *M. newberryi* to include these "extra" plates. Morphologically, the dental plates represent the functional region of the inferognathal in a juvenile mylostomatid, having a very thin and narrow attachment with the blade of the inferognathal. This functionally weak attachment between the two areas in this bone may be a result of either an extremely early growth stage or a pathologic condition, the latter being here suggested as an explanation for the abnormal osteological conditions in the jaw elements of the dinichthyid *Hussakofia* (Cossmann).

Branson (1914) described *Mylostoma eastmani* on the basis of an isolated posterior palatopterygoid from the Famennian Grassy Creek Shale of Louisiana, Missouri. This specimen, along with an element referred to by him as an "occipital" (= nuchal) of *Dinichthys rowleyi* (correctly identified as a *Dinognathus*-like median gnathal by Dunkle and Bungart, 1945), comprises the only known occurrence of *Mylostoma* outside the Ohio Shale Formation. The character-states established by Branson (1914) for *Mylostoma eastmani* are undiagnostic since they do not differ from those of *M. variabile*, and we therefore include *Mylostoma eastmani* as a synonym of *Mylostoma variabile*. This occurrence, however, extends the distribution of this genus outside of the Appalachian Basin onto the mid-continent.

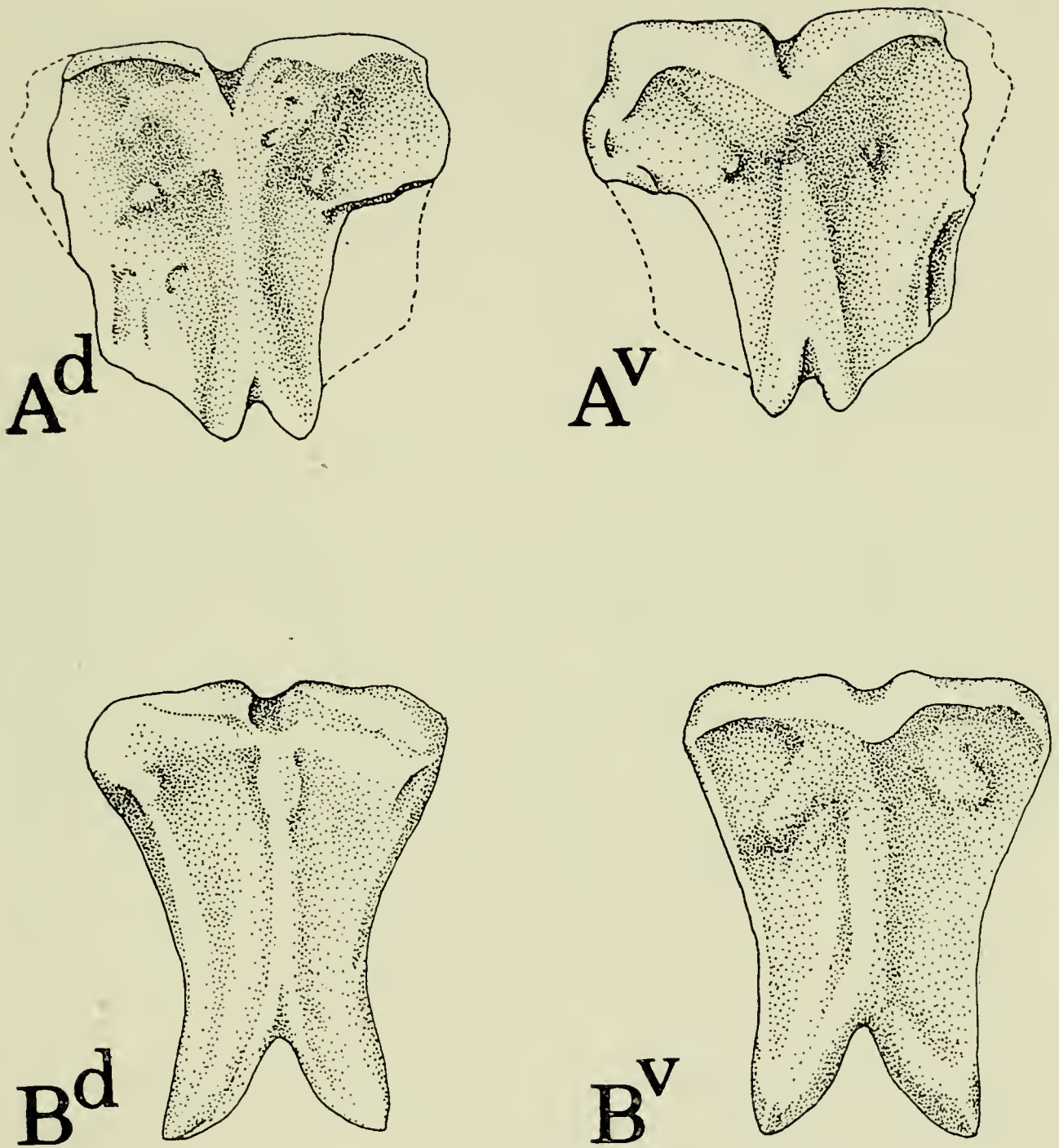


Figure 1. Median gnathal elements (after Dunkle and Bungart, 1945): A, *Mylostoma* (= *Dinognathus*) *eurhinus* CMNH 5063; B, *Mylostoma variable* (= *Dinognathus ferox*) CMNH 6094; d = dorsal, v = ventral.

Hussakof (1909: 268) described *Dinognathus ferox* (Fig. 1B) from a single median gnathal (AMNH 7915) resembling the mylostomatid dentition but having uncertain affinities. Eastman (1909) felt that *D. ferox* represented the fused part of the anterior palatopterygoids of an adult *Mylostoma*, but he lacked the appropriate specimens needed to prove this hypothesis. Dunkle and Bungart (1945), in describing *Dinognathus eurhinus* from a median gnathal (CMNH 5063; Fig. 1A), did not advocate Eastman's ideas on fusion of the anterior palatopterygoids and opposed his hypothesis on anatomical grounds, which they felt were contradictory to the generalized pattern of jaw elements in all arthrodiran fish. They considered his reconstruction of the *Dinognathus* median gnathal as a dorsal gnathal element of *Mylostoma* to be invalid, arguing that the median gnathal could not have been derived from the fusion of the anterior pair of mylostomatid palatopterygoid elements.

A recently discovered specimen (CMNH 8129; Plate 2) represents a complete set of gnathal elements belonging to an adult *M. variable*. This specimen consists of typical right and left inferognathals, right and left posterior palatopterygoids, and a *Dinognathus ferox* median gnathal. The discovery of this specimen, which lacks the anterior palatopterygoids but has posterior palatopterygoids and inferognathals associated with the *D. ferox* median gnathal element, confirms Eastman's hypothesis that the median gnathal of *D. ferox* represents the fusion of the anterior palatopterygoids in the adult mylostomatid (Fig. 2). A survey of all known existing mylostomatid palatal dental plates shows them to fall into three size categories: (1) the posterior palatopterygoids, having a size-growth range from juvenile to adult, (2) the anterior palatopterygoids, all representing juvenile specimens of varying degrees but none approaching the adult size of their corresponding posterior palatopterygoids, and (3) the median gnathals or fused anterior palatopterygoids, which all correspond to the adult size of the inferognathals and posterior palatopterygoids of the genus *Mylostoma*.

In view of this evidence, it is suggested here that the taxonomy of the Mylostomatidae may be revised as follows: the genus *Dinognathus* becomes a synonym of *Mylostoma*; *Mylostoma variable*, the type species, includes also *Dinognathus ferox*, *Mylostoma terrelli*, and *Mylostoma eastmani* as synonyms; "*Dinognathus*" *eurhinus* becomes a valid species of *Mylostoma*; *Mylostoma newberryi*, a species known only from the anterior portions of its inferognathals, is included within the Mylosto-

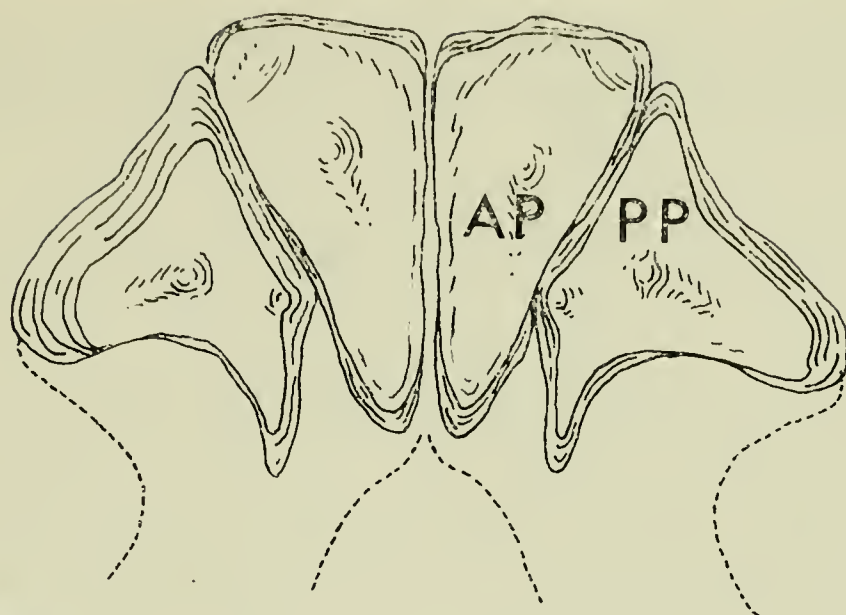
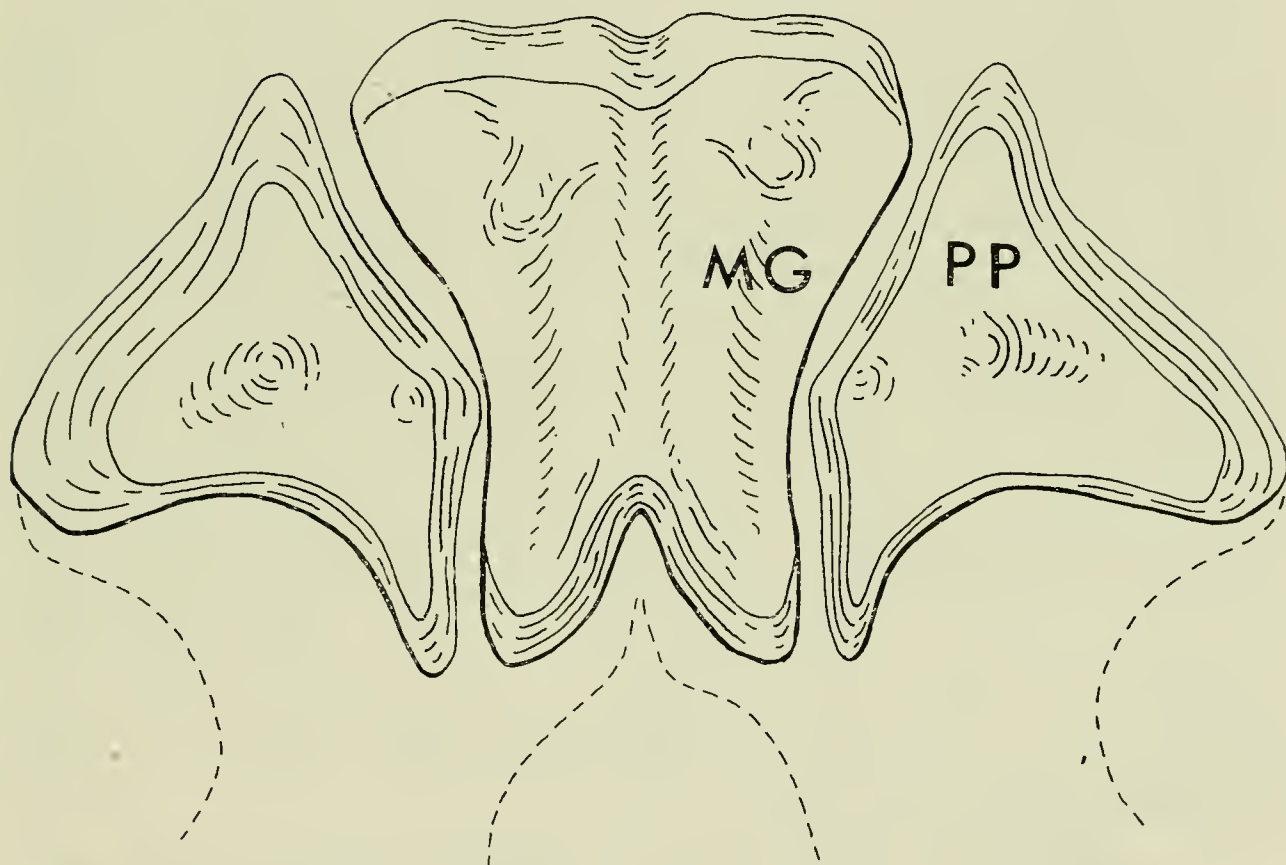
**A****B**

Figure 2. A, Eastman's (1907) reconstruction of the upper jaw apparatus of *Mylostoma variable*, displaying the paired anterior palatopterygoids (AP) of the juvenile condition (reconstruction based on AMNH 42G-43G, 3591, and MCZ 1437); B, Reconstruction of the upper jaw apparatus of *Mylostoma variable*, displaying the median gnathal (MG) of the adult condition (fused anterior palatopterygoids; reconstruction based on CMNH 8129); PP = posterior palatopterygoids.

matidae but its affinities with the other species of *Mylostoma* cannot be determined until additional material becomes available.

COMPARISON WITH OTHER ARTHRODIRES HAVING A SIMILAR JAW APPARATUS

As presently constituted, the family Mylostomatidae embraces the following genera: *Mylostoma* (= *Dinognathus*), *Dinomylostoma*, and possibly *Tafilalichthys*. Eastman (1906) described *Dinomylostoma*, which is restricted to the medial Frasnian Shales of New York and Kentucky, as being phylogenetically the most primitive of the mylostomatids. Although incompletely known, it is morphologically and chronologically transitional between *Dinichthys* and *Mylostoma*. The inferognathal elements possess a flat, narrow oral surface, not yet expanded as in *Mylostoma*. The blade-length comprises approximately 45 percent of the inferognathal, displaying the generalized condition of the adductor mandibulae muscles in the Frasnian mylostomatids, as compared to the 60 percent blade-length attained by the arched forward inferognathal elements of the Famennian *Mylostoma*. According to Dunkle and Bungart (1943), this specialized condition increases the length of the adductor mandibulae muscles to produce a more powerful bite. The anterior dorsal gnathal elements of *Dinomylostoma* display features transitional between the dinichthyid anterior supragnathals and the mylostomatid anterior palatopterygoids. The posterior gnathal elements, however, have become completely specialized into well-defined mylostomatid posterior palatopterygoids. This gnathal condition is paralleled to a less specialized degree by the Frasnian pholidosteid *Malerosteus*, described by Kulczycki (1957) from the Holy Cross Mountains of Poland.

It is interesting to note that the enigmatic arthrodire *Bungartius perissus* Dunkle, which is known from a single complete adult specimen, lacks the anterior supragnathal element. The jaw elements preserved represent the corresponding right and left inferognathals, the posterior supragnathals, and a well-developed median gnathal. In this case, Dunkle (1947: 104) considered the "anterior supragnathal element either vestigial or completely absent." The absence of the anterior supragnathal elements in the adult *Bungartius* parallels the absence of these elements in the adult *Mylostoma*. The median gnathal is uniquely restricted to these two genera and we believe it has developed

through the fusion of the anterior supragnathal elements during growth. This condition may occur also in the selenosteid *Paramylostoma* Dunkle and Bungart, in which the jaw mechanism is represented by an inferognathal specialized for crushing, and an associated posterior supragnathal. The anterior supragnathal and/or median gnathal is unknown in this genus.

The gnathal condition, suggesting a durophagous habit, while not exclusively restricted to the Mylostomatidae as demonstrated by *Bungartius*, *Paramylostoma*, and *Malerosteus*, has achieved its highest degree of specialization in the genus *Mylostoma*. This gnathal condition as manifested within other families of arthrodires is believed to represent diverse attempts of broader adaptation and efficiency of the feeding mechanisms at the pachyosteo-morph level of organization as suggested by Miles (1969).

On the basis of an isolated cranium, Lehman (1956) described *Tafilalichthys lavocati* as a new brachythoracid arthrodire from the Famennian of Southern Morocco. Obruchev (1964), in his review of this genus, suggested that *Tafilalichthys lavocati* might be a mylostomatid, since the cranium is morphologically similar to that of *Mylostoma* as described by Dean (1901). No gnathal elements are yet known from *T. lavocati*, and therefore no positive assignment to the Mylostomatidae can be made at this time. However, the close relationship of the North American Famennian arthrodiran taxa to the Moroccan arthrodiran remains, as well as a review of the Cleveland Shale Arthrodira, will be of considerable interest in documenting the phylogenetic and paleozoogeographic relationships within the Mylostomatidae.

The stratigraphic range of *Mylostoma* is relatively short, restricted to the Famennian (Late Devonian) time in North America. At this time the brachythoracid arthrodires achieved their highest level of adaptive radiation before extinction.

ACKNOWLEDGMENTS

Thanks are due to J.-P. Lehman and Daniel Goujet (Muséum National d'Histoire Naturelle, Paris), Farish A. Jenkins, Jr. and Robert H. Denison (Museum of Comparative Zoology), Richard Estes (Boston University), and William E. Scheele (Cleveland Museum of Natural History) for their helpful suggestions. This research was supported in part by grants from the Albion Foundation and Sigma Xi to Hlavin.

LITERATURE CITED

- BRANSON, E. 1914. The Devonian fishes of Missouri. Univ. Missouri Bull., 15 (31) : 59-74.
- DEAN, B. 1901. On the characters of *Mylostoma* Newberry. Mem. New York Acad. Sci., 2 (3) : 101-109.
- DUNKLE, D. 1947. A new genus and species of arthrodiran fish from the Upper Devonian Cleveland Shale. Cleveland Mus. Nat. Hist. Sci. Publ., 8 (10) : 103-117.
- , AND P. BUNGART. 1943. Comments on *Diplognathus mirabilis* Newberry. Cleveland Mus. Nat. Hist. Sci. Publ., 8 (7) : 73-84.
- , AND ———. 1945. Preliminary notice of a remarkable arthrodiran gnathal plate. Cleveland Mus. Nat. Hist. Sci. Publ., 8 (9) : 97-102.
- EASTMAN, C. 1906. Structure and relations of *Mylostoma*. Bull. Mus. Comp. Zool., 50 (1) : 1-29.
- . 1907. Mylostomid dentition. Bull. Mus. Comp. Zool., 50 (7) : 211-228.
- . 1909. Mylostomid palatal dental plates. Bull. Mus. Comp. Zool., 52 (14) : 261-269.
- HUSSAKOF, L. 1909. The systematic relationships of certain American arthrodiures. Bull. Amer. Mus. Nat. Hist., 26: 263-272.
- KULCZYCKI, J. 1957. Upper Devonian fishes from the Holy Cross Mountains (Poland). Acta Pal. Polonica, 2 (4) : 285-380.
- LEHMAN, J.-P. 1956. Les arthrodiures du Dévonien Supérieur du Tafilalet (Sud marocain). Notes Mém. Serv. Géol. Maroc., 129: 1-70.
- MILES, R. 1969. Features of placoderm diversification and the evolution of the arthrodire feeding mechanism. Trans. Roy. Soc. Edinburgh, 68 (6) : 123-170.
- NEWBERRY, J. 1883. Some interesting remains of fossil fishes, recently discovered. Trans. New York Acad. Sci., 2: 144-147.
- . 1889. The Paleozoic fishes of North America. Monog. U.S. Geol. Surv., 16: 1-340.
- OBRUCHEV, D. 1964. Class Placodermi. In Osnovy Paleontologii 11. Moscow: Nauka, pp.168-260.



Plate 1. *Mylostoma variable* (displaying cranial, thoracic, and ventral shields), juvenile: A, MCZ 1490; B, counterpart AMNH 7526; SO = sub-orbital.

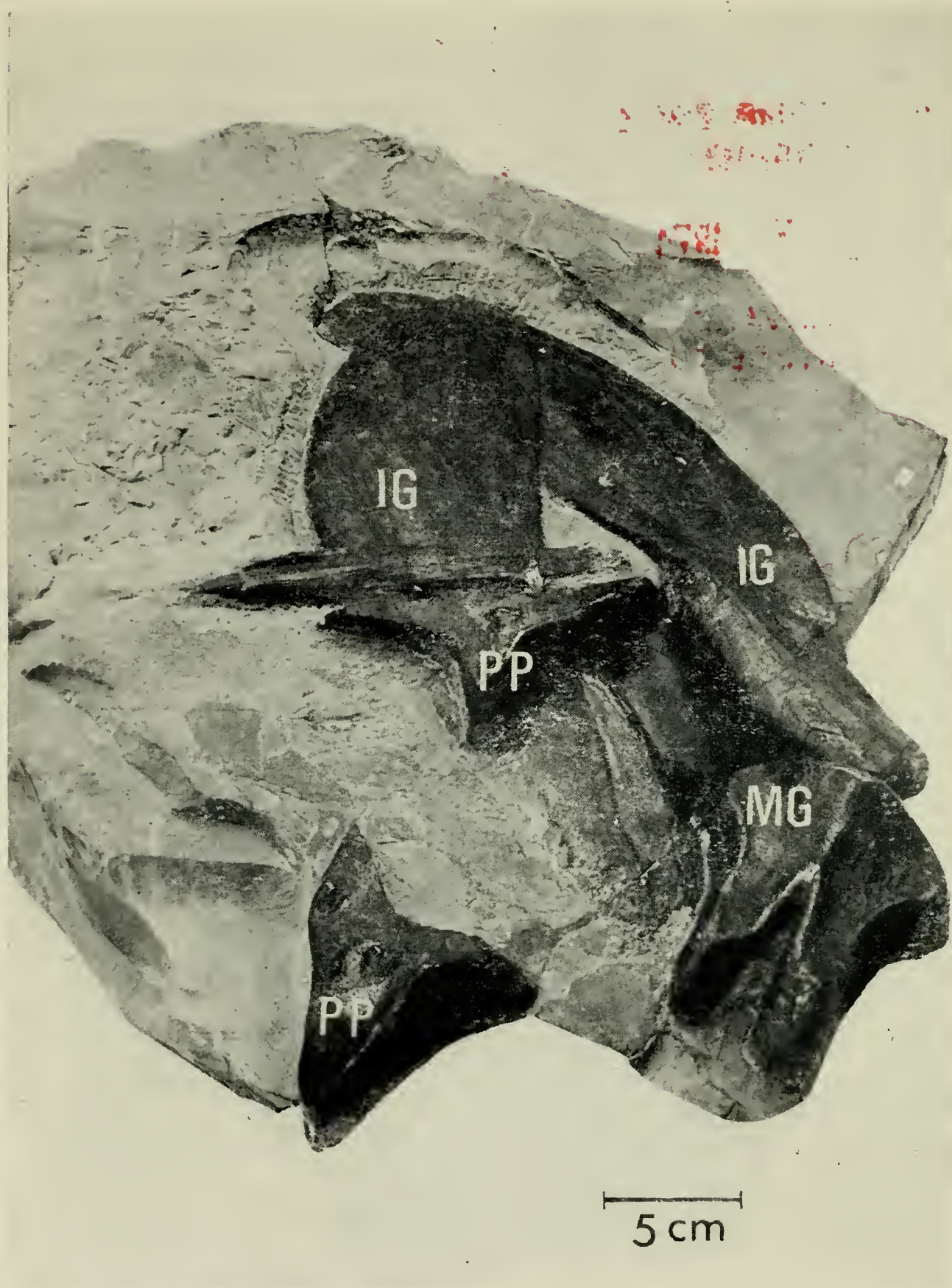


Plate 2. *Mylostoma variable* CMNH 8129; jaw elements of an adult showing left and right inferognathals (IG), left and right posterior palatopterygoids (PP), and a median gnathal = fused anterior palatopterygoids (MG).